Some Mathematical Considerations on Parent-Offspring Conflict Phenomenon(Mathematical Topics in Biology)

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Some Mathematical Considerations on Parent-Offspring Conflict Phenomenon

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子の独立時期についての親子間衝突に関する数理モデル解析

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A stochastic dynamic programming model for parent-offspring confict is analyzed and discussed. It is discussed how the conflict is resolved and how the ultimate offspring's independence age is determined between parent and offspring. Results by the mathematical model indicates such possibility that the observed behaviour of parental care may change depending on the parent's age. This is because the compromise conclusion of the parent-offspring conflict depends on the parent's age, that is essentially, on the parent's expected future reproductive value. Moreover, it is shown that the observed parent-offspring conflict possibly depends on the parent's age, too.

INTRODUCTION

In behavioural ecology, many researchers have been interested in and have discussed the parent-offspring conflict phenomenon: offspring wants to become independent of parent and to feed by itself after an age t_o^*, while parent of its age a wants to stop feeding after an offspring's age $t_p^*(a)$. The critical day $t_p^*(a)$ from the parent's viewpoint is assumed to depend on the parent's age a. When t_o^* and $t_p^*(a)$ do not coincide with each other, a conflict takes place between parent and offspring. There are possibly two different types of such conflict: $t_o^* < t_p^*(a)$; $t_o^* > t_p^*(a)$. Under the conflict in the case when $t_o^* < t_p^*(a)$, offspring wants to become independent of parent, while parent wants to feed offspring. On the other hand, in the case when $t_o^* > t_p^*(a)$, offspring wants to be fed, while parent wants to stop feeding. Only when $t_o^* = t_p^*(a)$, any conflict doesn't take place. However, since t_o^* does not depend on the parent's age a, whereas $t_p^*(a)$ does, the conflict between parent and offspring is observable very much.

In this work, we analyze a stochastic dynamic programming model which corresponds to the model constructed by Clark and Ydenberg (1990). In our model, differently from their model, parent is assumed to have a finite reproducible age-span, so that its future reproductive value is explicitly variable depending on the parent's age. A specific growth function and a specific terminal fitness function are introduced. Analyzing the model, we discuss the characteristics of the optimal critical ages t_o^* and $t_p^*(a)$, and it is shown that possibly existent conflict is only the type that $t_o^* > t_p^*(a)$, independently of the parent's age and the other parameters characterizing the relation between parent and offspring. Further, we discuss how the conflict is resolved and how the ultimate independence age is determined between parent and offspring.

MODEL

Parent's and Offspring's Ages

Let a denote the parent's age, for instance, in year, where $a_f \leq a \leq a_l$. a_f and a_l are respectively the first and the last ages for the parent's

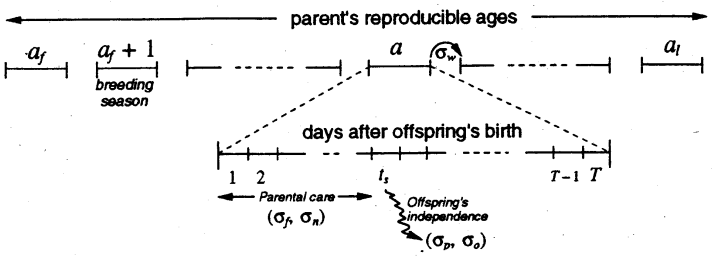


Fig. 1. Modelling the parent-offspring relation.

reproduction. Hence, the reproducible age-span for every parent is given by $a_l - a_f + 1$. The offspring's age *in day* during a breeding season is denoted by t, where $1 \leq t \leq T$. T is the length in day of breeding season (see Fig. 1).

Offspring's Growth

We use the following specific growth function for offspring:

$$Y(t+1) = \begin{cases} Y(t) + k_1 \\ \quad \text{for } t = 1, 2, \ldots, t_s - 1 \\ Y(t) + k_2 \\ \quad \text{for } t = t_s, t_s + 1, \ldots, T - 1 \end{cases} \quad (1)$$

$$Y(1) = Y_1, \quad (2)$$

that is,

$$Y(t) = \begin{cases} k_1(t-1) + Y_1 \\ \quad \text{for } t = 1, 2, \ldots, t_s \\ k_2(t - t_s) + k_1(t_s - 1) + Y_1 \\ \quad \text{for } t = t_s + 1, t_s + 2, \ldots, T, \end{cases} \quad (3)$$

where $Y(t)$ is the offspring's weight at the beginning of day t, and Y_1 is the offspring's weight at its birth. t_s is the offspring's age when parent stops feeding and offspring becomes independent. k_1 is a positive constant which means the offspring's daily growth rate with the parent's feeding, while k_2 is a positive constant which means the independent offspring's daily growth rate (see Fig. 2).

Now, consider the offspring's weight $Y(T; t_s)$ at the beginning of the last day T of the breeding season, under the condition that offspring becomes independent at day t_s. From (3), $Y(T; t_s)$ is expressed as follows:

$$Y(T; t_s) = k_2(T - t_s) + k_1(t_s - 1) + Y_1. \quad (4)$$

Offspring's Fitness

We define the daily survival probability σ_n for offspring fed by parent, the daily survival probability σ_o for offspring independent of parent, the daily survival probability σ_f for parent feeding offspring, and the daily survival probability σ_p for parent not feeding offspring (see Fig. 1). As Ydenberg (1989) showed in general for alcids, it is naturally assumed that $\sigma_o < \sigma_n$ and $\sigma_f < \sigma_p$. The following events significant to determine the offspring's fitness are assumed on each day: (i) If parent survives and feeds offspring with probability σ_f, offspring grows following to (3) with its survival probability σ_n; (ii) If parent dies with probability $1 - \sigma_f$, offspring becomes independent to grow following to (3) with its survival probability σ_o; (iii) If parent stops feeding offspring with its survival probability σ_p, offspring becomes independent to grow following to (3) with its survival probability σ_o.

Consider such probability $\phi(Y(T; t_s))$ that offspring with weight $Y(T; t_s)$ at the end of the breeding season will survive *after* the breeding season and reach the reproducible age to reproduce the next generation. The probability $\phi(Y(T; t_s))$ is called the *terminal fitness function* for offspring, and given as follows:

$$\phi(Y(T; t_s)) = \begin{cases} \gamma(Y(T; t_s) - y_c) \\ \quad \text{if } Y(T; t_s) > y_c; \\ 0 \quad \text{otherwise,} \end{cases} \quad (5)$$

where γ is a positive constant translating the advantage of weight gain $Y(T; t_s) - y_c$ to the probability $\phi(Y(T; t_s))$. y_c is the offspring's minimum body weight at the end of the breeding season, sufficient to survive *after* the breeding season and reach its reproducible age to reproduce the next generation (see Fig. 3).

Conventionally, we define the critical day t_c such that $Y(T; t_c) = y_c$, which is given by

$$t_c \equiv \frac{y_c - Y_1 + k_1 - k_2 T}{k_1 - k_2}. \quad (6)$$

Used the notation t_c, the probability $\phi(Y(T; t_s))$ can be expressed in the following way:
When $k_1 > k_2$,

$$\phi(Y(T; t_s)) = \begin{cases} \gamma(k_1 - k_2)(t_s - t_c) \\ \quad \text{if } t_s > t_c; \\ 0 \quad \text{otherwise.} \end{cases} \quad (7)$$

When $k_1 < k_2$,

$$\phi(Y(T; t_s)) = \begin{cases} \gamma(k_2 - k_1)(t_c - t_s) \\ \quad \text{if } t_s < t_c; \\ 0 \quad \text{otherwise.} \end{cases} \quad (8)$$

Eventually, it is assumed that $1 < t_c < T$. In the case when $k_1 > k_2$, if the offspring's independence day t_s is earlier than the critical day $[t_c] + 1$ given by (6), the offspring's weight $Y(T; t_s)$ at the end of the breeding season is below y_c so that the terminal fitness function $\phi(Y(T; t_s)$ is zero (Fig. 3). In contrast, in the case when $k_1 < k_2$, if the offspring's independence day t_s is later than $[t_c]$, the terminal fitness function $\phi(Y(T; t_s)$ is zero.

Now, we consider the offspring's fitness $F_o(t_s)$ defined as such probability that offspring can survive *through* and *after* the breeding season and reach its reproducible age to reproduce the next

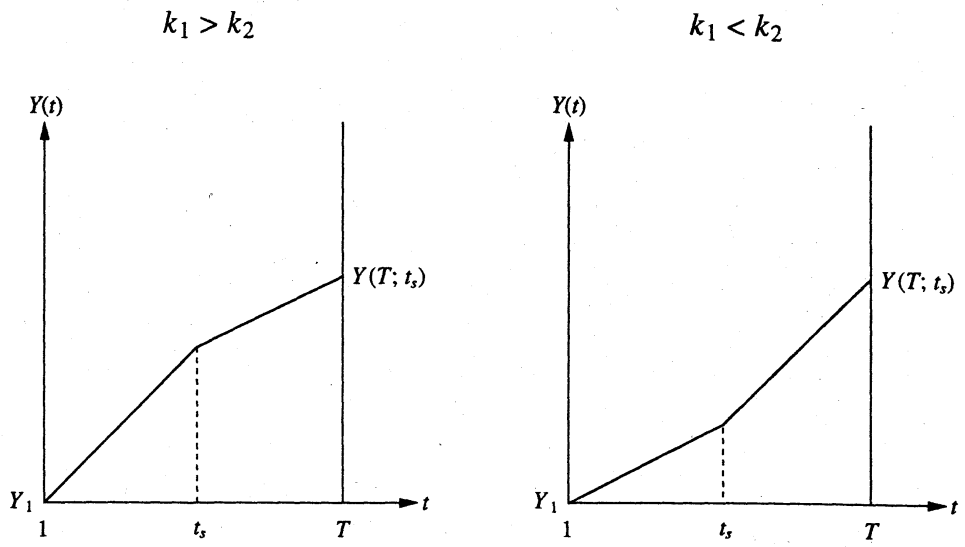


Fig. 2. Offspring's growth function $Y(t)$ for two cases: when $k_1 > k_2$ and the growth rate is larger under the parent's feeding than after the offspring's independence; when $k_1 < k_2$ and the growth rate has the inverse nature. Offspring has the weight Y_1 at its birth. If offspring becomes independent of parent on the day t_s, it reaches the weight $Y(T; t_s)$ at the end of the breeding season.

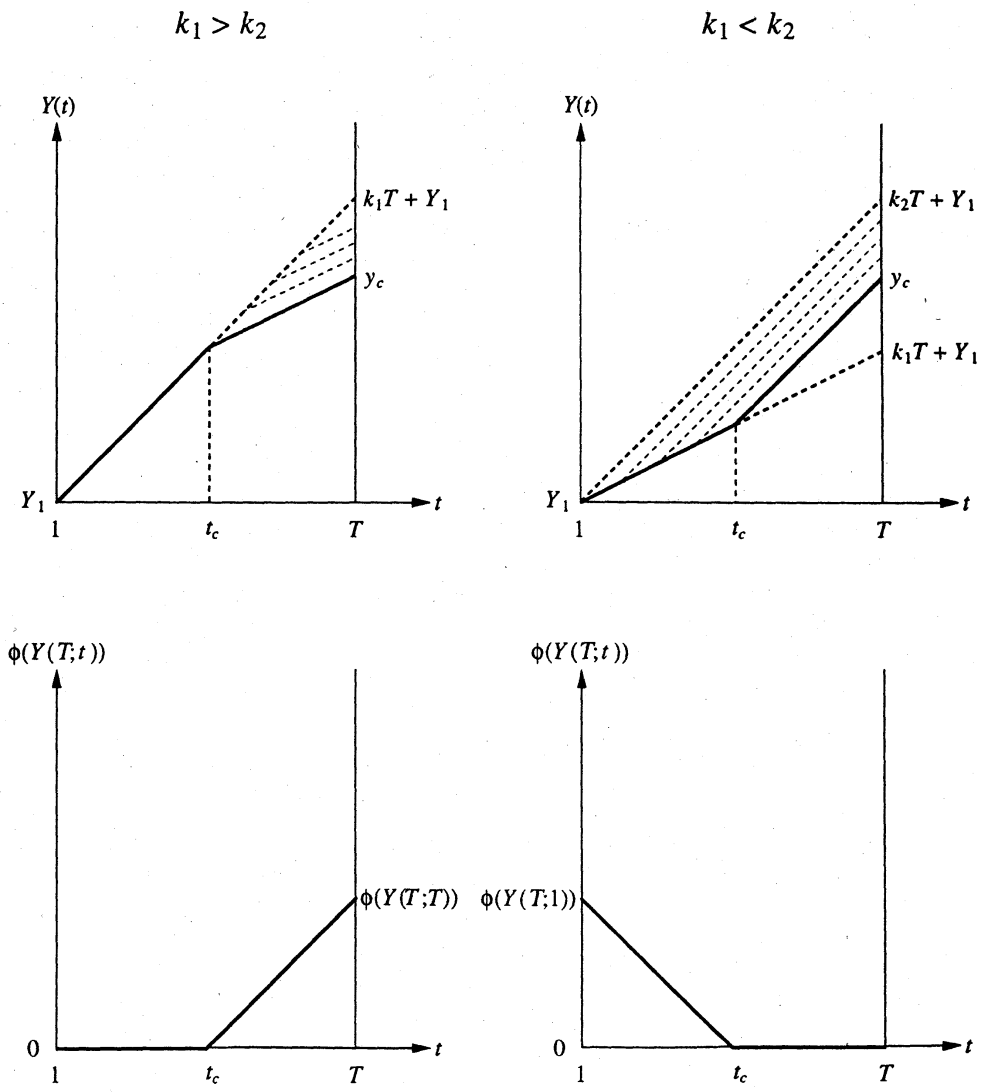


Fig. 3. Terminal fitness function $\phi(Y(T; t))$ given by (5). There exists such a critical day for the offspring's independence that the terminal fitness function $\phi(Y(T; t))$ is zero for any independence day t before or after the critical day.

generation, under the condition that it becomes independent on day t_s of the breeding season. If offspring becomes independent on the first day, that is, $t_s = 1$, it survives *through* the breeding season with probability σ_o^T. Growing up with (3), the offspring's weight reaches $Y(T;1)$ at the last day T of the breeding season, which means that, *after* the breeding season, offspring gets the probability $\phi(Y(T;1))$ to survive and reach its reproducible age. Hence, the offspring's fitness $F_o(1)$ is given by

$$F_o(1) = \sigma_o^T \phi(Y(T;1)). \tag{9}$$

In the case when $t_s = 2$, two cases arise to be considered. The first case is that, if parent dies on the first day with probability $1 - \sigma_f$, offspring is not fed by parent on any day *through* the breeding season. Thus, offspring is always independent and survives *through* the breeding season with probability σ_o^T. Therefore, the fitness in this case is given by $F_o(1)$ with probability $1-\sigma_f$. The second case is that, if parent survives and feeds offspring on the first day with probability σ_f, offspring is fed and survives for one day with probability σ_n. For $t_s = 2$, offspring becomes independent on the second day. Then, the independent offspring survives *through* the rest of the breeding season with probabilty σ_o^{T-1}. The offspring's weight reaches $Y(T;2)$ on day T, which means that, *after* the breeding season, offspring gets the probability $\phi(Y(T;2))$ to survive and reach its reproducible age. Lastly, the offsping's fitness $F_o(2)$ is given by

$$\begin{aligned} F_o(2) = {} & (1-\sigma_f)\sigma_o^T \phi(Y(T;1)) \\ & + \sigma_f \sigma_n \sigma_o^{T-1} \phi(Y(T;2)). \end{aligned} \tag{10}$$

In the case when $t_s = 3$, three cases arise. The first case is that parent dies on the first day with probability $1 - \sigma_f$. The second case is that parent survives on the first day with probability σ_f and dies on the second day with probability $1 - \sigma_f$. In this case, from the second day, offspring becomes independent and survives *through* the rest of the breeding season with probability σ_o^{T-1}. The third case is that parent survives and feeds offspring on both of the first and the second days with probability σ_f^2. In this case, offspring survives for two days with probability σ_n^2. For $t_s = 3$, offspring becomes independent on the third day. The independent offspring survives *through* the rest of the breeding season with probability σ_o^{T-2}. Lastly, the offspring's fitness $F_o(3)$ is given by

$$\begin{aligned} F_o(3) = {} & (1-\sigma_f)\sigma_o^T \phi(Y(T;1)) \\ & + \sigma_f(1-\sigma_f)\sigma_n \sigma_o^{T-1} \phi(Y(T;2)) \\ & + \sigma_f^2 \sigma_n^2 \sigma_o^{T-2} \phi(Y(T;3)). \end{aligned} \tag{11}$$

For the case when $t_s = 4, 5, ..., T$, $F_o(t_s)$ is given in the same way.

Consequently, except for the case when $t_s = 1$, $F_o(t_s)$ is expressed in general as follows:

$$\begin{aligned} F_o(t_s) = {} & \sum_{j=1}^{t_s-1} \sigma_f^{j-1}(1-\sigma_f)\sigma_n^{j-1}\sigma_o^{T-j+1}\phi(Y(T;j)) \\ & + \sigma_f^{t_s-1}\sigma_n^{t_s-1}\sigma_o^{T-t_s+1}\phi(Y(T;t_s)). \end{aligned} \tag{12}$$

Parent's Survival Probability

In this section, We consider the parent's survival probability $F_p(t_s)$, which is defined as such probability that parent survives through the breeding season under the condition that it stops feeding on day t_s in the breeding season. Now, σ_w is defined as such probability that parent survives through the interval period between two sequent breeding seasons and reaches the next breeding season.

If parent never feeds offspring on any day through the breeding season, that is, if $t_s = 1$, parent survives through the breeding season with probability σ_p^T. Then, parent can reach the next breeding season with probability σ_w. Hence, the parent's survival probability $F_p(1)$ is given by

$$F_p(1) = \sigma_p^T \sigma_w. \tag{13}$$

If parent feeds offspring on the first day and stops feeding on the second day, that is, if $t_s = 2$, parent survives on the first day with probability σ_f and through the rest of the breeding season with probability σ_p^{T-1}. Hence, the parent's survival probability $F_p(2)$ is given by

$$F_p(2) = \sigma_f \sigma_p^{T-1} \sigma_w. \tag{14}$$

In the case when $t_s = 3$, two cases arise to be considered. The first case is that parent feeds offspring on the first day with its survival probability σ_f, while offspring dies on the first day with probability $1 - \sigma_n$. Then, parent survives through the rest of the breeding season with probability σ_p^{T-1}. The second case is that parent feeds offspring on the first day with its survival probability σ_f, while offspring survives on the second day with its survival probability σ_n. Parent feeds offspring also on the second day with its survival probability σ_f. For $t_s = 3$, parent stops feeding on the third day. Then, parent survives through the rest of the breeding season with probability σ_p^{T-2}. Lastly, the parent's survival probability $F_p(3)$ is given by

$$F_p(3) = \{(1-\sigma_n)\sigma_f\sigma_p^{T-1} + \sigma_n\sigma_f^2\sigma_p^{T-2}\}\sigma_w. \quad (15)$$

For the case when $t_s = 4, 5, ..., T$, $F_p(t_s)$ is given in the same way.

Consequently, except for the case when $t_s = 1$ or $t_s = 2$, $F_p(t_s)$ is expressed in general as follows:

$$\begin{aligned} F_p(t_s) &= \sigma_w \sum_{j=1}^{t_s-2} \sigma_n^{j-1}(1-\sigma_n)\sigma_f^j\sigma_p^{T-j} \\ &\quad + \sigma_w\sigma_n^{t_s-2}\sigma_f^{t_s-1}\sigma_p^{T-t_s+1}. \end{aligned} \quad (16)$$

MODEL

Parent's Fitness

Consider the parent's fitness at its age a, under the condition that it stops feeding on day t_s of the breeding season. The parent's fitness $J(t_s; R(a))$ is defined by the parent's survival probability $F_p(t_s)$, its offspring's fitness $F_o(t_s)$, and the parent's expected future reproductive value $R(a)$ at the last day of the breeding season at the parent's age a, which satisfies the following:

$$\begin{aligned} R(a) &= \sigma_w J(t_s; R(a+1)) \\ &\quad (a = a_f, a_f+1, \ldots, a_l-1) \end{aligned} \quad (17)$$

$J(t_s; R(a+1))$ means the parent's fitness at its age $a+1$. Since σ_w means the probability that parent survives between the end of the breeding season at its age a and the beginning of the next breeding season at its age $a+1$, the righthand side of (17) means the expected future reproductive value. Remark that $R(a)$ should be monotonically decreasing in terms of the age a, and $R(a_l) = 0$ because a_l is the last age for the parent's reproduction.

As in Clark and Ydenberg (1990), $J(t_s; R(a))$ is given in this paper as follows:

$$J(t_s; R(a)) = F_o(t_s) + R(a)F_p(t_s). \quad (18)$$

From (17) and (18), we can obtain the backward recurrence equation to determine the expected future reproductive value $R(a)$ for every age a. It is assumed that, since the expected future reproductive value $R(a)$ is considered only for parent to determine its behaviour $t_p^*(a)$ from its viewpoint, it has no relation with t_o^* from the offspring's viewpoint. Thus, since $R(a_l) = 0$, the expected future reproductive value $R(a_l - 1)$ for the age $a_l - 1$ is determined by

$$\begin{aligned} R(a_l-1) &= \sigma_w J(t_p^*(a_l); R(a_l)) \\ &= \sigma_w F_o(t_p^*(a_l)), \end{aligned} \quad (19)$$

and, further, in general, the value $R(a_l - i)$ $(i = 1, 2, ..., a_l - a_f)$ for the age $a_l - i$ is given by the following backward recurrence equation:

$$R(a_l - i) = \sigma_w J(t_p^*(a_l - i + 1); R(a_l - i + 1)). \quad (20)$$

ANALYSIS

The Optimal Offspring's Independence Age From The Offspring's Viewpoint

The optimal offspring's independence age t_o^* from offspring's viewpoint is defined as the day to maximize the offspring's fitness $F_o(t_s)$ in the breeding season. Therefore, by analyzing $F_o(t_s)$ given by (9) and (12) (as for the way of analysis, see Appendix A), t_o^* can be obtained as follows (Fig. 4):

When $k_1 > k_2$,

$$t_o^* = T. \quad (21)$$

When $k_1 < k_2$,

$$t_o^* = \begin{cases} 1 & \text{if } t_c < \nu + 2; \\ n & \text{if } \nu + n < t_c \le \nu + n + 1 \\ & \quad (n = 2, 3, \ldots, T-1), \end{cases} \quad (22)$$

where

$$\nu \equiv \frac{1}{\sigma_n/\sigma_o - 1}. \quad (23)$$

Since $\sigma_n > \sigma_o$ from the assumption, $0 < \nu < \infty$. For convenience, we will hereafter use the notation ν.

As seen in Fig. 4, those conditions for t_o^* in the case when $k_1 < k_2$, given by (22), are complementary each other, and the possibly maximal $F_o(t_s)$ is $T-1$ in the case.

The Optimal Offspring's Independence Age From Parent's Viewpoint

The optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint is defined as the offspring's age t_s to maximize the parent's fitness $J(t_s; R(a))$. By analyzing $J(t_s; R(a))$ given by

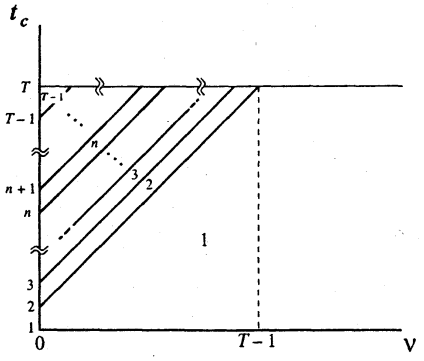


Fig. 4. In the case when $k_1 < k_2$, the optimal offspring's independence age t_o^* from the offspring's viewpoint on the parameter space (v, t_c). For $1 < t_c < T$, $t_o^* < T$.

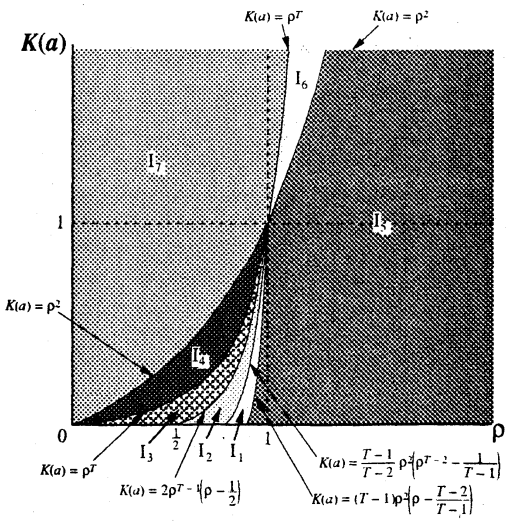


Fig. 5. In the case when $k_1 > k_2$, the parameter space (ρ, $K(a)$) is categorized into $I_1 \sim I_7$, depending on the type of the division of the parameter space (v, t_c) in terms of the value of $t_p^*(a)$.

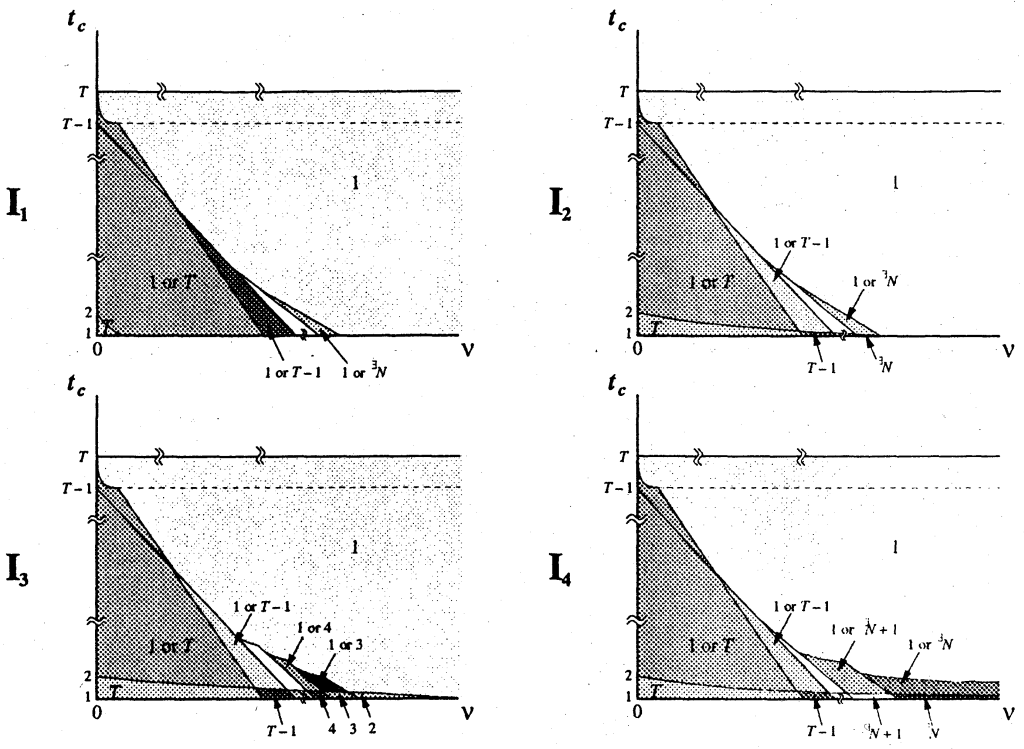


Fig. 6. In the case when $k_1 > k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint on the parameter space (v, t_c) for the parameter sets $I_1 \sim I_4$ of the parameter space (ρ, $K(a)$).

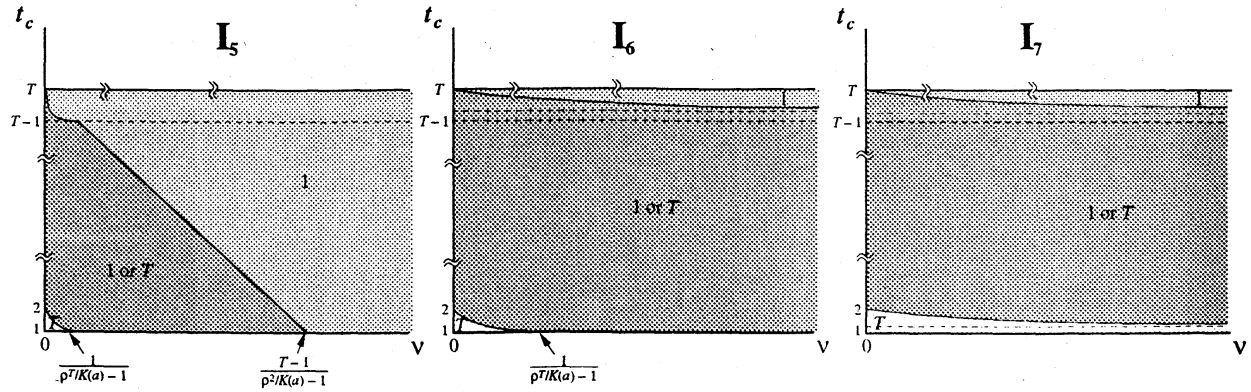


Fig. 7. In the case when $k_1 > k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint on the parameter space (v, t_c) for the parameter sets $I_5 \sim I_7$ of the parameter space (ρ, $K(a)$).

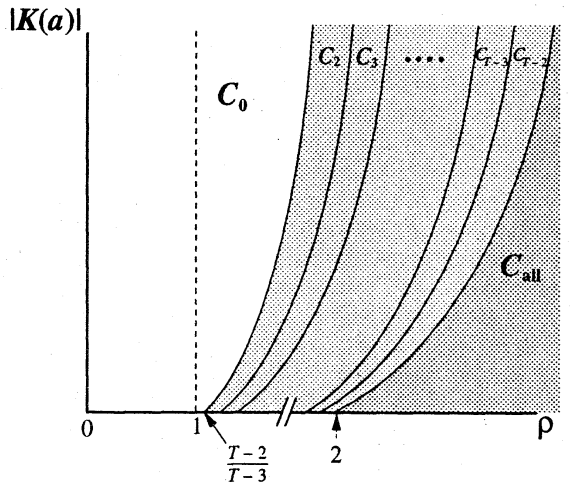
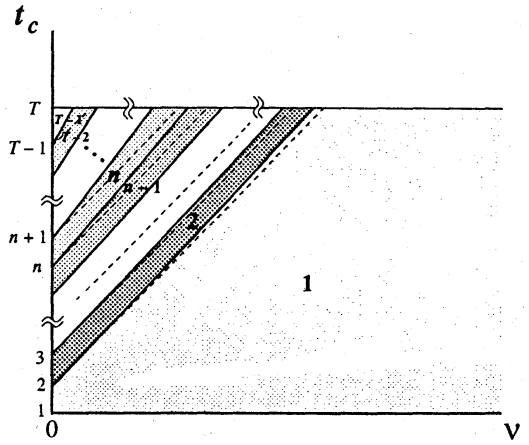
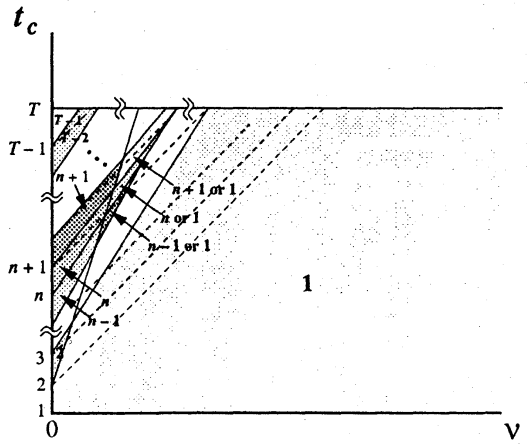


Fig. 8. In the case when $k_1 < k_2$, the parameter space $(\rho, |K(a)|)$ is categorized into C_0, C_{all}, and $C_2 \sim C_{T-2}$, depending on the type of the division of the parameter space (ν, t_c) in terms of the value of $t_p^*(a)$.





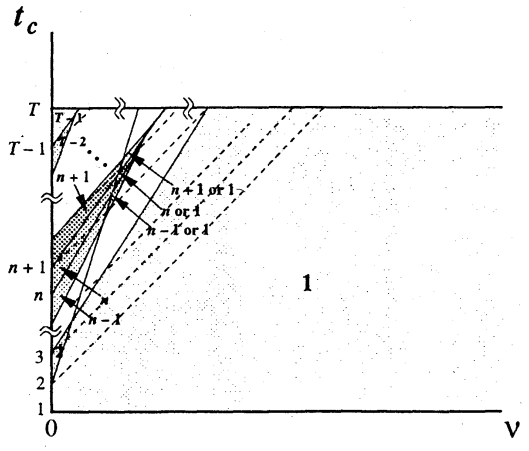


Fig. 9. In the case when $k_1 < k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint on the parameter space (ν, t_c) for the parameter sets, C_0, C_{all}, and C_n $(n = 2, 3, ..., T-2)$ of the parameter space $(\rho, |K(a)|)$.

(18), $t_p^*(a)$ can be obtained for the parent's age a, when $R(a) > 0$, that is, when $a_f \le a \le a_l - 1$, as follows:

When $k_1 > k_2$,

$$t_p^*(a) = \begin{cases} 1 & \text{if } t_c > g_2(\nu;a); \\ n & \text{if } n-1 \le t_c < n \\ & \quad \text{and } h_{n+1}(\nu;a) \le t_c < g_n(\nu;a), \\ & \text{or if } t_c < n-1 \\ & \quad \text{and } h_{n+1}(\nu;a) \le t_c < h_n(\nu;a) \\ & \quad (n = 2,3,\ldots,T-1); \\ T & \text{if } T-1 \le t_c < T \\ & \quad \text{and } t_c < g_T(\nu;a), \\ & \text{or if } t_c < T-1 \\ & \quad \text{and } t_c < h_T(\nu;a). \end{cases} \quad (24)$$

When $k_1 < k_2$,

$$t_p^*(a) = \begin{cases} 1 & \text{if } t_c < h_1(\nu;a); \\ n & \text{if } h_n(\nu;a) < t_c \le h_{n+1}(\nu;a) \\ & \quad (n = 2,3,\ldots,T-1), \end{cases} \quad (25)$$

where

$$g_n(\nu;a) \equiv n + \frac{\rho^{T-n+2}}{K(a)} \frac{\nu}{\nu+1} \quad (26)$$

$$h_n(\nu;a) \equiv n + \left(1 - \frac{\rho^{T-n+2}}{K(a)}\right)\nu \quad (27)$$

$$\rho \equiv \frac{\sigma_p}{\sigma_o} \quad (28)$$

$$K(a) \equiv \frac{\gamma(k_1-k_2)}{R(a)} \frac{\sigma_p/\sigma_w}{\sigma_p/\sigma_f - 1}. \quad (29)$$

Note that those conditions for $t_p^*(a)$ are not complementary each other. For example, in the case when $k_1 > k_2$, there exist such parameters that $g_2(\nu;a) < t_c < h_T(\nu;a) < T-1$. This means that, with such parameters, $t_p^*(a)$ should be 1 *or* T. In this case, $t_p^*(a)$ can be ultimately determined by comparing $J(1;R(a))$ with $J(T;R(a))$. In this paper, avoiding a mess of calculations, we no longer discuss the ultimately determined $t_p^*(a)$ in such case, because our presented analyses give sufficiently significant qualitative results valuable for the discussion on the parent-offspring conflict phenomenon.

As indicated by those conditions for $t_p^*(a)$, given by (24) and (25), the ultimately determined $t_p^*(a)$ strongly depends on parameters (Fig. 6, Fig. 7, Fig. 9). The parameter space (ν, t_c) can be devided into some subregions depending on what value is possible for $t_p^*(a)$. The way of the devision depends on the other parameters ρ and $K(a)$ (Fig. 5, Fig. 8).

In the case when $k_1 > k_2$, depending on the type of the division of the parameter space (ν, t_c), we categorize the paremeter region of $(\rho, K(a))$ into those regions $I_1 \sim I_7$ as shown in Fig. 5 (as for the analyzing way, see Appendix B). According to those parameter subregions of $(\rho, K(a))$, the ultimately determined $t_p^*(a)$ is shown in the parameter space (ν, t_c) as in Fig. 6 and Fig. 7. In cases of I_1, I_2, and I_4, the possible value of $t_p^*(a)$ is T or less than an N, while, in case of I_3, it is any value from 1 to T. In cases of $I_5 \sim I_7$, only 1 or T is possible for $t_p^*(a)$.

In contrast, in the case when $k_1 < k_2$, we categorize the paremeter region of $(\rho, |K(a)|)$ into those regions C_0, C_n $(n = 2,3,\ldots,T-2)$, and C_{all} as shown in Fig. 8 (Appendix B). For those regions, the ultimately determined $t_p^*(a)$ is shown in the parameter space (ν, t_c) as in Fig. 9. Independently of which case is considered, any value from 1 to $T-1$ is possible for $t_p^*(a)$.

When $a = a_l$, since $R(a_l) = 0$ from the definition, it is followed that $J(t_s; R(a_l)) = J(t_s; 0) = F_o(t_s)$. Therefore, $t_p^*(a_l) = t_o^*$ given by (21) and (22), and there does not occur any conflict between parent and offspring.

The offspring's independence age $\tilde{t}_p$ to maximize the parent's survival probability $F_p(t_s)$ is always 1 independently of the values of parameters, because $F_o(t_s)$ is monotonically decreasing. Indeed, since $\sigma_p > \sigma_f$, for any t_s,

$$F_p(t_s+1) - F_p(t_s) = \sigma_n^{t_s-1}\sigma_f^{t_s-1}\sigma_p^{T-t_s}(\sigma_f - \sigma_p)\sigma_w < 0. \quad (30)$$

From the definition (18), when parent is sufficiently young and $R(a)$ is so large, it is expected that $t_p^*(a)$ is near $\tilde{t}_p$, because $J(t_s; R(a)) \approx R(a)F_p(t_s)$. Indeed, as seen in Fig. 6, Fig. 7, and Fig. 9, the parameter region for $t_p^*(a) = \tilde{t}_p = 1$ is relatively larger for the smaller $|K(a)|$ than for the larger.

Existence of Parent-Offspring Conflict

Compared Fig. 4 to Fig. 6, Fig. 7, and Fig. 9, the parent-offspring confict presents for a wide range of parameters.

In the case when $k_1 > k_2$, as shown in Fig. 6 and Fig. 7, especially for relatively large value of t_c, the parent-offspring conflict can exist, because $t_o^* = T$. The type of conflict is eventually for $t_o^* > t_p^*(a)$, that is, under conflict, parent tends to stop feeding its offspring, while offspring wants to be fed. Only for sufficiently small values of t_c and ν, $t_o^* = t_p^*(a) = T$, and, all over the breeding season,

parent keeps feeding its offspring who wants to be fed.

As well, in the case when $k_1 < k_2$, as shown in Fig. 9, only one type of conflict, $t_o^* > t_p^*(a)$, is possible to exist and occur. This result can be easily proved that any slope of boundaries of parameter regions in (ν, t_c), given by (27), is more than 1.

Parent's Age Dependence of Conflict

The optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint for a breeding season is determined depending on the value of $K(a)$, that is, of $R(a)$ as shown by the above analysis. Following the definition, $|K(a)|$ is monotonically increasing to infinite as the parent's age a increases, since $R(a)$ monotonically decreases as a increases, and reaches zero at the age a_l. Therefore, as the parent's age increases, the parameter point moves up in the parameter space $(\rho, |K(a)|)$.

In the case when $k_1 > k_2$ and $0 < K(a)$, if $\rho \geq 1$, as the parent's age increases, the parameter point $(\rho, K(a))$ moves as $I_5 \rightarrow I_6 \rightarrow I_7$ in Fig. 5. Therefore, since $t_o^* = T$ in this case, whenever the conflict occurs, $t_p^*(a) = 1$, and parent tends to stop feeding its offspring on everyday of the breeding season, while offspring wants to be fed all over the breeding season. Otherwise, when the conflict does not occur, then parent keeps feeding its offspring all over the breeding season. Moreover, for some parameters of (ν, t_c), as seen in Fig. 7, the conflict does not occur for parent older than a critical age determined by the parameter $(\nu, t_c$, while the conflict occurs for the younger parent.

If $\rho < 1$ when $k_1 > k_2$, as the parent's age increases, the parameter point $(\rho, K(a))$ moves up in Fig. 5 through the following order of parameter regions in it: $I_5 \rightarrow I_1 \rightarrow I_2 \rightarrow I_3 \rightarrow I_4 \rightarrow I_7$. The parameter point $(\rho, K(a))$ does not pass any region with any order inverse to this order. The argument similar to that for $\rho \geq 1$ is applicable for this case. As the parent's age increases, $t_p^*(a)$ tends to be the same or to increase, therefore, it is likely that, after a critical parent's age, the conflict does not occur and parent keeps feeding all over the breeding season.

As mentioned before, at the parent's age a_l last in the reproducible age span, in the case when $k_1 > k_2$, the conflict does not occur and $t_p^*(a) = t_o^* = T$, so that parent keeps feeding all over the breeding season.

It is concluded for the case when $k_1 > k_2$ that the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint stays the same or tends to become the larger toward T as the parent's age a increases, and the conflict of the type for $t_o^* > t_p^*(a)$ disappears after a parent's age, then, parent keeps feeding all over the breeding season.

On the other hand, in the case when $k_1 < k_2$ and $K(a) < 0$, as the parent's age a increases, the parameter point $(\rho, |K(a)|)$ moves up in Fig. 8 through the following order of parameter regions in it: $C_{all} \rightarrow C_{T-2} \rightarrow C_{T-3} \rightarrow \cdots \rightarrow C_3 \rightarrow C_2 \rightarrow C_0$. The parameter point $(\rho, |K(a)|)$ does not pass any region with any order inverse to this order. Therefore, as seen in Fig. 9, since the conflict is only of the type that $t_o^* > t_p^*(a)$, the conflict can disappear after a critical age of parent for some parameters of (ν, t_c). For the other parameters of (ν, t_c), the conflict of type that $t_o^* > t_p^*(a)$ occurs through the parent's reproducible age-span except for the last age a_l. In both cases, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint stays the same or tends to become the larger as the parent's age a increases, as well as in the case when $k_1 > k_2$.

Resolution of Parent-Offspring Conflict

By the above analysis, it is shown that the parent-offspring conflict possibly occurs depending on those parameters including the parent's age. The conflict is resolved once parent or offspring yields to another. In this section, we discuss how the conflict is resolved, and how the compromised day $t^*(a)$ when offspring becomes independent is determined.

For the resolution of parent-offspring conflict, the cost for conflict is taken into account. Now, the cost for conflict is assumed to be introduced as the decrease of fitness (Higashi and Yamamura, 1993). That is, under the conflict, it is assumed that offspring must pay a cost c to counter parent, while parent must pay a cost αc to counter offspring, where c is monotonically increasing as the duration of the behaviour to counter another side per conflict, and α is a positive constant. At the beginning of any day under the conflict situation, $c = 0$ because the behaviour to counter another side is not yet started. Those costs are subtracted from fitnesses of parent and offspring.

In the following, we consider the resolution of parent-offspring conflict, making use of the cost

mentioned above, for two distinct cases: $t_o^* > t_p^*(a)$; $t_o^* < t_p^*(a)$.

CASE A: $t_o^* > t_p^*(a)$

The compromised day $t^*(a)$ naturally satisfies that $t_p^*(a) \leq t^*(a) \leq t_o^*$. The fitness gain $D_p(t;a)$ for parent on a day t under the conflict (expected for the case in which parent wins the conflict and succeeds in making offspring independent), relative to such fitness that parent yielded to offspring in the first place and let offspring depending on the parent's feeding, is now given by

$$D_p(t;a) = J(t;R(a)) - J(t+1;R(a)) - \alpha c. \quad (31)$$

On the other hand, the fitness gain $D_o(t;a)$ for offspring on a day t under the conflict (expected for the case in which offspring wins the conflict and succeeds in making parent feeding), relative to such fitness that offspring yielded to parent in the first place and became independent, is now given by

$$D_o(t;a) = F_o(t+1;a) - F_o(t;a) - c. \quad (32)$$

When $t_p^*(a) \leq t < t^*(a)$, the fitness gains $D_p(t;a)$ and $D_o(t;a)$ must eventually decline from positive toward zero on the day t, because the cost c is temporally increasing as the behaviour of conflict continues. Therefore, when $D_p(t;a)$ becomes zero while $D_o(t;a)$ is still positive, parent yields to offspring and feeds it. Thus, when $t_p^*(a) \leq t < t^*(a)$, there exists such a value of c that $D_p(t;a) = 0$ and $D_o(t;a) > 0$. On the other hand, on the day when $t = t^*(a)$, parent does not yield to offspring before offspring yields to parent, from the definition of $t^*(a)$. This means that there exists such a value of c that $D_o(t;a) = 0$ and $D_p(t;a) \geq 0$. It is assured that $t^*(a) \leq t_o^*$, because $D_o(t_o^*;a) \leq -c$ from the definition of t_o^* so that the compromised independence day does not be beyond the day t_o^*. This argument can be simplified with the following function $\theta(t;\alpha,a)$:

$$\begin{aligned}\theta(t;\alpha,a) &\equiv \alpha\{F_o(t+1;a) - F_o(t;a)\} \\ &\quad + \{J(t+1;R(a)) - J(t;R(a))\} \\ &= (\alpha+1)\{F_o(t+1;a) - F_o(t;a)\} \\ &\quad + R(a)\{F_p(t+1;a) - F_p(t;a)\} \\ &= (\alpha+1)\left\{J(t+1;\tfrac{R(a)}{\alpha+1}) - J(t;\tfrac{R(a)}{\alpha+1})\right\}.\end{aligned} \quad (33)$$

Remark that $\theta(t;\alpha,a) > 0$ when $t_p^*(a) \leq t < t^*(a)$, while $\theta(t;\alpha,a) \leq 0$ when $t = t^*(a)$. Therefore, the compromised day $t^*(a)$ is given by

$$t^*(a) = \min_t\{t|\theta(t;\alpha,a) \leq 0, t_p^*(a) \leq t \leq t_o^*\}. \quad (34)$$

CASE B: $t_o^* < t_p^*(a)$

As before, the compromised day $t^*(a)$ naturally satisfies that $t_o^* \leq t^*(a) \leq t_p^*(a)$. Contrarily to CASE A, the fitness gain $D_p(t;a)$ for parent on a day t under the conflict (expected for the case in which parent wins the conflict and succeeds in keeping offspring under the parent's feeding), relative to such fitness that parent yielded to offspring in the first place and let offspring independent, is now given by

$$D_p(t;a) = J(t+1;R(a)) - J(t;R(a)) - \alpha c. \quad (35)$$

The fitness gain $D_o(t;a)$ for offspring on a day t under the conflict (expected for the case in which offspring wins the conflict and succeeds in becoming independent), relative to such fitness that offspring yielded to parent in the first place and accepted the parent's feeding, is now given by

$$D_o(t;a) = F_o(t;a) - F_o(t+1;a) - c. \quad (36)$$

By the same argument as in CASE A, when $t_o^* \leq t < t^*(a)$, there exists such a value of c that $D_p(t;a) > 0$ and $D_o(t;a) = 0$. On the day when $t = t^*(a)$, there exists such a value of c that $D_o(t;a) \geq 0$ and $D_p(t;a) = 0$. Also in this case, it is assured that $t^*(a) \leq t_p^*(a)$, because $D_p(t_p^*(a);a) \leq -\alpha c$ from the definition of $t_p^*(a)$. This argument can be simplified with the same function (33), $\theta(t;\alpha,a)$. Moreover, the compromised day $t^*(a)$ is given by the following equation similar to (34):

$$t^*(a) = \min_t\{t|\theta(t;\alpha,a) \leq 0, t_o^* \leq t \leq t_p^*(a)\}. \quad (37)$$

We note that, since the considered signiture of $\theta(t;\alpha,a)$ is determined by the difference of $J(t;R(a)/(\alpha+1))$, $t^*(a)$ is regarded as the smallest value that gives the maximal of $J(t;R(a)/(\alpha+1))$ when $\min\{t_o^*, t_p^*(a)\} \leq t \leq \max\{t_o^*, t_p^*(a)\}$. Existence of such $t^*(a)$ is assured by the above argument.

By the result for our model, it is shown that the conflict is only of the type that $t_o^* > t_p^*(a)$, that is, of CASE A, and as the parent's age a increases and the expected future reproductive value $R(a)$ decreases, $t_p^*(a)$ stays the same or becomes the larger and approaches t_o^* from below. Therefore, the above result indicates that the compromise between parent with the expected future reproductive value $R(a)$ and its offspring shifts the offspring's independence day to that corresponding to the favorable (not necessarily optimal!) independence age from the viewpoint of parent with the expected future reproductive value $R(a)/(\alpha+1)$. Eventually, the compromised independence day $t^*(a)$ is the nearer to t_o^* as α is the larger.

In the case when $k_1 > k_2$ and $\rho \geq 1$, $t_o^* = T$ and $t_p^*(a)$ is 1 or T, as resulted in the previous section (Fig. 7). Thus, the compromise can cause only two alternative conclusion of the parent-offspring conflict: offspring becomes independent on the first day of breeding season, or parent keeps feeding offspring all over the breeding season. Since $t_p^*(a)$ is 1 or T by our analysis, if parent yields to offspring on the first day of breeding season, the offspring's independence does not occur until the last day of breeding season.

On the other hand, in the case when $k_1 > k_2$ and $\rho < 1$, the compromise can cause the offspring's independence on the day $t^*(a)$ such that $1 < t^*(a) < T$ (see Fig. 6). Depending on the parameters, the compromise conclusion same as in the case when $k_1 > k_2$ and $\rho \geq 1$ still possibly occurs.

In the case when $k_1 < k_2$, both of t_o^* and $t_p^*(a)$ can take any value less than T, depending on the parameters, whereas it is always satisfied that $t_o^* > t_p^*(a)$, as resulted in the previous section (Fig. 9). Therefore, the compromise can cause the offspring's independence on the day $t^*(a)$ as defined as $t_p^*(a) \leq t^*(a) \leq t_o^*$.

CONCLUSION

Results by our mathematical model indicates such possibility that the observed behaviour of parental care may change depending on the parent's age. This is because the compromise conclusion of the parent-offspring conflict depends on the parent's age, that is essentially, on the parent's expected future reproductive value. Moreover, the observed parent-offspring conflict possibly depends on the parent's age, too.

As long as in the framework of our mathematical model, the possibly observed parent-offspring conflict is of the type that $t_o^* > t_p^*(a)$, that is, parent intends to stop feeding its offspring, while offspring wants to be fed. Hence, if another type that $t_o^* < t_p^*(a)$, that is, parent intends to feed, while offspring wants to become independent, is observed, some improved mathematical model will be required for the mathematical theoretic explanation on it.

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APPENDIX A

In this appendix, we show the way to determine analytically t_o^* and $t_p^*(a)$. The optimal offspring's independence age t_o^* from offspring's viewpoint is defined as the day to maximize the offspring's fitness $F_o(t_s)$ in the breeding season. Thus, t_o^* should be one of maximals of $F_o(t_s)$ for $t_s = 1, 2, ..., T$. The necessary condition for $t_o^* = 1$ is

$$F_o(2) - F_o(1) < 0.$$

In the same way, the necessary condition for $t_o^* = T$ is

$$F_o(T) - F_o(T-1) > 0,$$

where it is assumed that, if $F_o(T) = F_o(T-1)$, then, $t_o^* \leq T - 1$. In contrast, the necessary condition for $t_o^* = n$ $(n = 2, 3, ..., T-1)$ is as follows:

$$\begin{cases} F_o(n) - F_o(n-1) > 0 \\ F_o(n+1) - F_o(n) \leq 0. \end{cases}$$

Some cumbersome analyses of those necessary conditions can lead to possible values of t_o^* given as (21) and (22).

Also as for $t_p^*(a)$, the same argument is adaptable for $J(t_s; R(a))$ given by (18). In this case, as long as is considered parent-offspring relation within a breeding season, the expected future reproductive value can be regarded as a non-negative constant independent of t_s. Therefore, the same way of analysis can be carried out for $J(t_s; R(a))$ and give those possible values of $t_p^*(a)$ as (24) and (25).

APPENDIX B

In this appendix, some outlines of analyzing way on the parameter dependence of the optimal offspring's independence age from parent's viewpoint, given by Fig. 5 and Fig. 8.

In the case when $k_1 > k_2$, t_p^* is given by (24). Function $g_n(\nu; a)$ has the following asymptote:

$$t_c = n - \frac{\rho^{T-n+2}}{K(a)}.$$

Therefore, depending on the position of the above asymptote, the valid condition of (24) switches, because the positional relation among those functions $g_n(\nu;a)$ and $h_n(\nu;a)$ changes (see Fig. A). Further, the positional relation depends also on n. Thus, as seen in cases of I_1, I_2, and I_4 of Fig. 6, there is such case that t_p^* cannot be less than ${}^3N > 1$. For $n < {}^3N$ in such case, the positional relation corresponds to (a) or (b) in Fig. A. As indicated in Fig. A, the positional relation can be analytically categorized by analyzing the positional relation among those points P_n and P_{n+1}, given by

$$P_n : \left(n-1, \frac{1}{\rho^{T-n+2}/K(a)-1}\right)$$

$$P_{n+1} : \left(n-1, \frac{2}{\rho^{T-n+1}/K(a)-1}\right).$$

If P_{n+1} is located left to P_n, there exists some region for $t_p^* = n$, seen in the case (d) of Fig. A. Even if P_{n+1} is located right to P_n, when $\rho < 1$, there can exist a region for $t_p^* = n$, seen as the case (e) in Fig. A, under the following condition:

$$\frac{n}{\rho^{T-n+1}/K(a)-1} < \frac{n-1}{\rho^{T-n+2}/K(a)-1}.$$

This condition means that the cross section of $h_{n+1}(\nu;a)$ on ν axis is located left to that of $h_n(\nu;a)$. In Fig. 5, no distinction is indicated between two cases (d) and (e) of Fig. A. Including these cases, the parameter region of $(\rho, K(a))$ further shows a detail structure, when $k_1 > k_2$, as shown in Fig. B: those regions I_3 and I_4 are respectively divided into distinct two regions. For parameters of I_{3U}, as increasing n for $t_p^* = n$, both cases of (d) and (e) occur in the order from (d) to (e) of Fig. A, while, for those of I_{3L}, only the case (d) occurs. Similarly, for parameters of I_{4U}, as increasing n, if $n < {}^3N$, the case (a) occurs, and when $n = {}^3N$, (c) occurs. Then, for $n > {}^3N$, both cases of (d) and (e) occurs from (d) to (e). However, for those of I_{4L}, the case (e) does not occurs, taken the place by (d). As another case, if the following condition is satisfied for ${}^3N$ when $\rho < 1$,

$$\frac{\rho^{T-N+2}}{K(a)} \le 1 < \frac{\rho^{T-N+1}}{K(a)},$$

there exist some region for $t_p^* = N$ as given by (c) in Fig. A. This case is included in the region I_4 of Fig. 5, as seen in Fig. 6.

In the case when $k_1 < k_2$, the same way can be carried out for $h_n(\nu;a)$ and $h_{n+1}(\nu;a)$. For C_n, the region of (ν, t_c)-space for $t_p^* = j$ less than $n+1$ and more than 1 appears as triangle because $h_n(\nu;a)$ and $h_{n+1}(\nu;a)$ cross, as in Fig. 9.

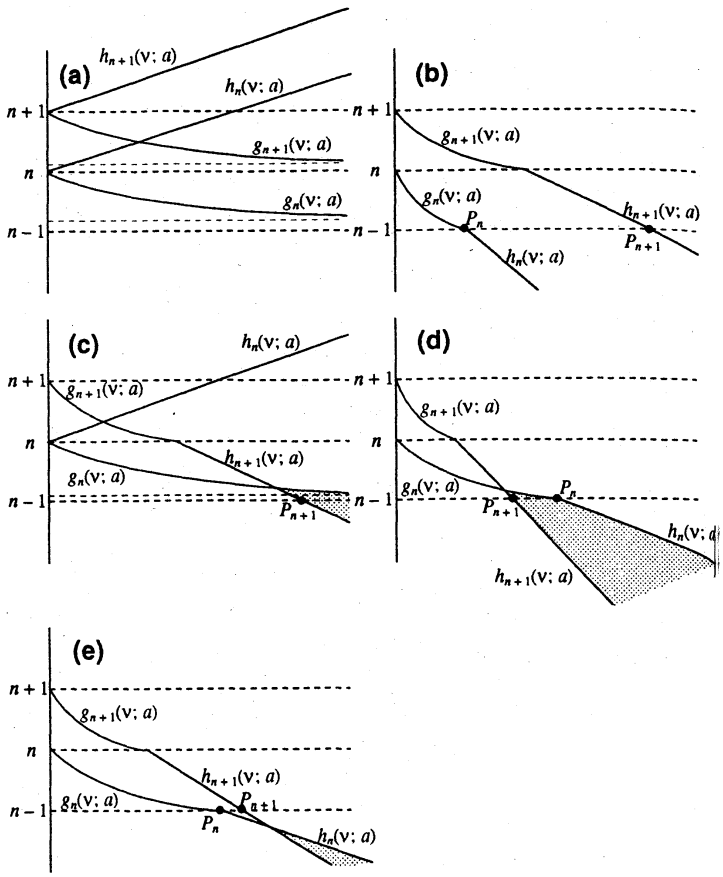

Fig. A. Schematic description of the configuration pattern for $g_n(\nu;a)$ and $h_n(\nu;a)$. For detail explanation, see text.

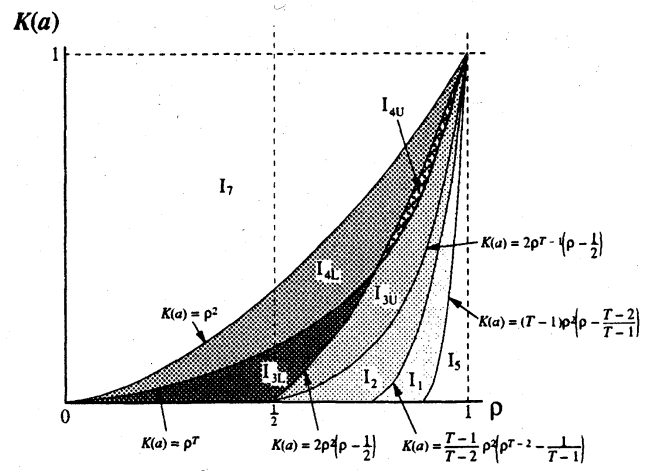

Fig. B. In the case when $k_1 > k_2$ and $\rho \le 1$, the parameter space $(\rho, K(a))$ consists of a detail structure depending on the type of the division of the parameter space (ν, t_c) in terms of the value of $t_p^*(a)$. Compare with Fig. 5.